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# An insight into advances in fisheries biology, genetics and genomics of African tilapia species of interest in aquaculture

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ABSTRACT

Morphological identification of tilapia species is complicated by extensive intraspecific variation of morphological characters used for classical identification. To address this obstacle, use of molecular techniques as additional tools for identification of these cichlids is recommended. Further, DNA marker technologies are useful in other areas such as conservation genetics, evolutionary biology, molecular ecology, population genetics, fish safety monitoring. A summary of the various methods of tilapia genetic resources characterization based on molecular markers is presented. We focused on some of tilapia species that are widely cultured in Africa, this includes both *Oreochromis niloticus* and *Sarotherodon melanotheron*. Eleven molecular markers that were divided into three categories (cytoplasmic, dominant and codominant markers) are commonly used for genetic analysis in tilapia, each has its advantages and disadvantages. Novel methods of genome sequencing and mapping in tilapia are also presented and discussed.

## 1. Introduction

Nowadays, fishery catches are declining in many countries. This is attributable to increased fishing exploitation, pollution, destruction of habitats, high mortality due to diseases, introduction of new species and climate change (Amoussou et al., 2017; Dudgeon et al., 2006; Ndiaye et al., 2010). In addition, aquaculture is facing several challenges, including lack of a sufficient number of genetically improved species, lack of species-specific feeds, high mortality due to diseases and pollution of ecosystems (Yue and Wang, 2017). When confronted with these fisheries threats, many countries regulate the exploitation of aquatic natural resources based mainly on stock abundance evaluations (proportional stock density, relative stock density, fishing effort, catch per unit effort, etc.) (Birkeland and Dayton, 2005; Gustafson, 1988) and neglect issues of their evolution and viability (Abban et al., 2004; Dudgeon et al., 2012; Nguyen et al., 2006b; Nikolic et al., 2009a). However, information contained in genes (e.g. difference in alleles, DNA sequences, …) can prove useful on that matter (Nikolic et al., 2009b, 2009a) as well as to design long-term sustainable conservation strategies.

Genetic markers (e.g. mtDNA, microsatellites, and NGS (Next Generation Sequencing) such as RAD-SEQ (Restriction-site Associated DNA Sequencing) or complete genomic studies) offer the great advantage of allowing direct assessment of genetic diversity. They are powerful instruments to detect genetic uniqueness of individuals, populations or species (Askari et al., 2013; Park and Moran, 1994). Their uses concern research on domestication, evolution, conservation, management of natural resources including impact of domesticated populations on wild populations and impact of exotic species introductions and improve stocks through marker assisted selection (Ferguson et al., 1995; Lazard, 2013; Liu and Cordes, 2004; Poompuang and Hallerman, 1997; Rognon et al., 1996; Romana-Eguia et al., 2004; Verrier and Rognon, 2000).

With at least 6000 fish species, perciformes represent the largest order of vertebrates. More than 1300 species of this order are in the family Cichlidae (Nelson, 2006), including over 70 species of tilapias (Trewavas, 1984). The cichlid fishes can be found in all inter-tropical regions of Africa, the Americas, and Asia and have undergone

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impressive adaptive radiation in East African lakes (Barlow, 2000; Brawand et al., 2014; Goldschmidt, 1996; Lee et al., 2005). Moreover, ecological variations are important in the structuring of natural cichlid fish populations since, for aquatic organisms, geographical isolation factors such as waterfalls and expanses of land can prevent the movement of individuals between populations and hence diminish gene flow (Crispo and Chapman, 2008).

The problems of tilapia genetic resources management are of three kinds: loss of species purity through mismanagement of interspecific hybridization, high levels of inbreeding depression and the contamination of genetically improved strains by introgression from wild species (Amoussou et al., 2017; Kocher et al., 1998; Lazard, 2013). Specifically, some genetic hazards are posed by introgression of cultured stocks into wild populations, which threatens the harm of disrupting local adaptations (Amoussou et al., 2017). With a view to addressing these issues, knowledge of extant genetic resources can prove essential for fisheries and aquaculture management (Falk et al., 2004; Hallerman and Hilsdorf, 2014). According to Appleyard et al. (2001), the significance of genetic polymorphisms in populations or stocks can be analysed by studying associations between fitness or performance traits and individual genotypics at both coding and non-coding regions of the genome. In addition, detecting associations between genotypes and performance traits may depend on allelic diversity, recombination rate and the degree of linkage disequilibrium observed in a population (Appleyard et al., 2001; Balloux et al., 2004; Mittell et al., 2015; Szulkin et al., 2010). Concerning tilapia species, current studies aim at improving fish performance and expanding the environmental tolerance regarding low temperatures and salinity (Amoussou et al., 2014; Cnaani et al., 2000; Ouattara et al., 2009a, b; Ouattara et al., 2005, 2003). A greater use of genetic markers of choice for the management of stocks, identification of quantitative trait loci (QTL), and improvement of strains through marker-assisted selection should be promoted (Cnaani et al., 2004; Cnaani and Hulata, 2011; Gupta et al., 2004; Poompuang and Hallerman, 1997).

The fish species *O. niloticus* and *S. melanotheron* constitute key commercial fish stocks in Africa. These two tilapia species are the most used in both fresh and brackish water tilapia farming in Africa (Gourène et al., 1999; Ouattara et al., 2009b, 2003; Toguyeni, 2004). However, comparative molecular genetic studies on populations of both *O. niloticus* and *S. melanotheron* from West Africa are missing. The systematics of these tilapias is based on morphological, ecological and behavioural characters. It can be very difficult to identify these species due to similar morphological features between species and large intraspecies morphological variation, additionally complicated by occasional hybridization events (Adépo-Gourène et al., 2006).

This review focuses on molecular markers that can be used in tilapia molecular genetics. Nevertheless, the use or not of a genetic marker depend on several factors and knowing them is important before operating the choice of research objectives. Each genetic marker has its quality-price ratio as well as advantages and disadvantages of handling. Operating a choice is also knowing the most reliable and promising genetic tools for tilapias characterization. Meanwhile, this paper aims at inventorying as well as yielding the most useful molecular biology techniques used to characterize tilapia species and/or stocks and describe their advantages and limitations as well as the current trends in their fisheries biology. The importance of tilapias in African fish farming is described first. Tilapia cytogenetics, sex-reversal, sex determination systems, and basic concepts in fish genetics are then discussed followed by the phylogeny of tilapia species, genome mapping and genome sequencing. Finally, genetic markers used and samplings made during different tilapia genetic diversity studies are discussed.

## 2. Importance of tilapias in African fish farming

In 2018, aquaculture production in Africa reached 1.99 millions tonnes, which represents 2.5% of the world's total production (FAO (Food and Agriculture Organization of the United Nations), 2018). Tilapia farming represents on average 20% of African Aquaculture (Abban and Agyakwa, 2004), and so becomes the type of aquaculture the most practiced in Africa (FAO (Food and Agriculture Organization of the United Nations), 2018, 2014, 2012). The subfamily of the tilapiine belongs to the Cichlidae Family and includes about 100 species grouped into three genera (*Oreochromis*, *Sarotherodon* and *Tilapia*) which differentiate themselves by their reproductive behavior and diet (Paugy et al., 2004; Trewavas, 1984). The main types used in aquaculture are *Oreochromis* and *Sarotherodon* (Amoussou et al., 2016), including four species that are now farmed on a significant scale: *O. niloticus*, *S. melanotheron*, *O. aureus*, *O. mossambicus*, and their hybrids (Ansah et al., 2014; FAO (Food and Agriculture Organization of the United Nations), 2010; Lazard, 2009; Li et al., 2006; Toguyeni et al., 2009). In the developing world, tilapia production is rising with a new market that targets national and regional consumers rather than international markets (FAO (Food and Agriculture Organization of the United Nations), 2014). It now represents the major source of income of African fish farmers (ADB, 2005; Adebo and Alfred, 2008). Their production is expected to be higher than 9.2 million tonnes in 2030 (FAO (Food and Agriculture Organization of the United Nations), 2014). Tilapias are of interest also because they have undergone a rapid and extensive speciation event (Chew et al., 2002) and thus also represent interesting model species for evolutionary ecology studies. Genetics and genomics of these tilapias are attracting more and more attraction, as they provide useful tools for strain management (Brawand et al., 2014; Cnaani et al., 2004; Cnaani and Hulata, 2011; Gupta et al., 2004; Lee et al., 2010; Soler et al., 2010).

## 3. Sex-reversal in tilapias

In tilapia species with high reproductive potential, responsiveness to sex-reversal treatment is a desired trait for the production and culture of monosex populations to control the overcrowding that results in reduced growth (Owusu-Frimpong et al., 2005). Thus, many aquaculture industry actors produce all-male populations to improve productivity and control reproduction, because males have superior growth rate, and unlimited size levels compared to females (Lind et al., 2015). Exogenous factors such as temperature and sex steroid can induce sex modifications when administered before and during sexual differentiation, i.e. 15 days post-fertilization (Baroiller et al., 1995; Bezault et al., 2007; Gennotte et al., 2014; Rougeot et al., 2008a, 2008b; Tessema et al., 2006; Wessels and Hörstgen-Schwark, 2011). The sex-reversal method allows partial or total masculinization and partial or total feminization of offspring whose phenotypes may be opposed to genotypes. The use of high rearing temperatures ($\approx 36$ °C) to modify the sex ratio of tilapia offspring is done during the 30 days post-resorption of the yolk-sac (Bezault et al., 2007). The thermal-sensitivity of sex differentiation fluctuates from one offspring group to another and depends on the genetic characteristics of the broodstock used (Baras et al., 2001; Tessema et al., 2006). The male and female sex steroids (testosterone *vs* estradiol) are administered either by injection or immersion or incorporation into fish feed (El-Sayed et al., 2012; Rougeot et al., 2008a). The efficiency of the hormonal sex-reversal depends on the period of application, duration of treatment, fish stocking density, and the nature and concentration of the hormone (Desprez et al., 2003; Gennotte et al., 2014). The major environmental factors influencing hormonal sex-reversal are temperature and dissolved oxygen (Baroiller et al., 1995; Beaven and Muposhi, 2012).

In aquaculture, several other methods such as hybridization, gynogenesis, androgenesis (Table 1) are used to obtain sex-reversed individuals.

### 3.1. Hybridization

Hybridization is used not only to improve fish productivity but also

**Table 1**
Comparison of some key methods used for sex-reversal in tilapias.

| Characteristics | Hybridization | Gynogenesis | Androgenesis | Source |
|---|---|---|---|---|
| Reproduction mode | Two breeders | Single breeder | Single breeder | Amoussou (2017); Bezault (2005); Carter et al. (1991); Felip et al. (2001); Liu (2007); Mair et al. (1991); Mélard (2015); Myers et al. (1995); Ouedraogo (2014) Peruzzi et al. (1993) Stickney (2005); Wohlfarth and Hulata (1981) |
| Genome involved | Paternal and maternal genomes | Maternal genome | Paternal genome | |
| Different types | Intraspecific | Endo-meiotic (by blocking the expulsion of the second polar body, during the resumption of meiosis; the resulting progeny includes heterozygous or homozygous genotypes) | – | |
| | Interspecific | Endo-mitotic (by blocking the first cytodiaeresis; the resulting progeny is totally homozygous) | Endo-mitotic (by blocking the first cytodiaeresis; the resulting progeny is totally homozygous) | |
| | Intergeneric | – | – | |
| Type of shock | – | Thermal shock or pressure | Thermal shock or pressure | |
| Type of inactivation | – | Sperm inactivated by UV irradiation | Ovum inactivated by UV irradiation | |
| Types of sex ratios | ZX male 1:0 or ZX, YW, YZ male and XW female 3:1 | XX female 0:1 or WW female and ZZ male 1:1 | Depends on the homogametic system (female (XX) or male (ZZ)) | |
| Advantage | Quite easy procedure | The technique can be used to produce completely homozygous individuals in the first generation | Best suited to male homogametic species | |
| Disadvantage | Possible negative impacts by escaping into the wild (i) Breeders contamination (ii) Low growth of hybrids (iii) Difficulties of care to "pure" broodstock lines | The technique is too demanding (i) Broods are very inbred (ii) | Not suitable for mass production (i) Not very reliable (ii) | |

to enhance viability and to create monosex populations, by obtaining individuals from either intraspecific or even interspecific or intergeneric crossing (Adöpo-Gourène et al., 2006; Bakhoum et al., 2009; Barton, 2001; Hutchings and Fraser, 2008; Mélard, 2015; Scribner et al., 2000; Tave et al., 1990; Toguyeni et al., 2009). In the fish species, the different levels of hybridization are detected by the Bayesian assignment. The first attempts to produce tilapia hybrids were made by crossing *O. mossambicus* and *O. hornorum* (Hickling, 1960), *O. niloticus* and *O. macrochir* (Jalabert et al., 1971), *O. niloticus* and *O. aureus* (Wohlfarth, 1994). Nowadays, some of these hybrids are commonly produced in aquaculture farms, but mainly to benefit from both good growth of *O. niloticus* and the best tolerance at low temperatures of *O. aureus*.

While hybridization is yield useful for aquaculture stocks (Hickling, 1960; Lahav and Lahav, 1990; Majumdar and McAndrew, 1983; Pruginin et al., 1975) it can have a negative impact on the fish stocks. Repeated crossing of hybrid individuals and parental species can further the introgression of genes from one species (or population) into the gene pool of another (Senanan et al., 2004). When natural hybrids are less fit or viable than the parental species, secondary contact results in reinforcement of the reproductive isolation and represents a phylogenetic dead end (D'Amato et al., 2007). In addition, tilapia hybrids can be affected by overdominance and heterosis.

Overdominance is a selective process in which the survival and/or fertility of an individual are increased if the individual is heterozygous at a given locus (De Meeûs, 2012; De Meeûs et al., 2007). Overdominance generates an excess of heterozygous individuals compared to Hardy–Weinberg expectations (De Meeûs et al., 2007). One of the most documented example is sickle cell anaemia against the malignant agent of malaria *Plasmodium falciparum* (Thomas et al., 2010). It can also occur in aquaculture (Fjalestad, 2005; Liu, 2007). Crossing two lines in which different alleles are fixed gives an F1 in which all individuals are heterozygous, and this is the only way of producing a group of individuals that are all heterozygous. In a non- inbred population no more than 50% of the individuals can be heterozygous for a particular pair of alleles (Fjalestad, 2005). In addition, overdominance can affect tilapia hybrids (*O. mossambicus* X *O. aureus*) traits (Cnaani et al., 2003). An increasing overdominance effect was observed for length, weight and cold tolerance in these hybrids as fish heterozygous for each marker were more cold tolerant and smaller than homozygous fish.

The heterosis or hybrid vigour or outbreeding enhancement appears when closely related species, subspecies or strains of the same species are crossed between themselves. This global phenomenon may affect the whole genome (De Meeûs et al., 2007). It tends to homogenize the allele frequencies between different sites (subpopulations) at all loci involved. The heterozygous individuals (at all or many loci) are favored (De Meeûs, 2012). The hybrid would have a much higher yield than either inbred parent (Hartl and Clark, 2007). The average value of the offspring for a particular trait would exceed the mean of the average values of the parental lines (Attipoe, 2006; Ruane et al., 2013). These hybrids often reveal improved performance compared to both parents for some characters such as growth, reproductive fitness, survival, feed conversion, cold or salinity tolerance, carcass quality and disease resistance (Barberousse et al., 2010; Bartley et al., 2001; Gupta et al., 2004; Ky et al., 2012; Neira et al., 2016; Nielsen et al., 2010). The heterosis is always maximum (100%) in the first generation, but a variable part of this effect is lost in subsequent generations (Wiener and Rouvier, 2009).

Superior performance of hybrids is a result of gene interactions and differences among alleles contributed by two distinct populations, inbred lines or species (Senanan et al., 2004). There are two methods generally used to estimate heterosis. The first one is to compare crossbred progenies with the average of the parental line/strain, the second is to compare the crossbred progenies with the average of the better parental line/strain (Fjalestad, 2005). The interspecific

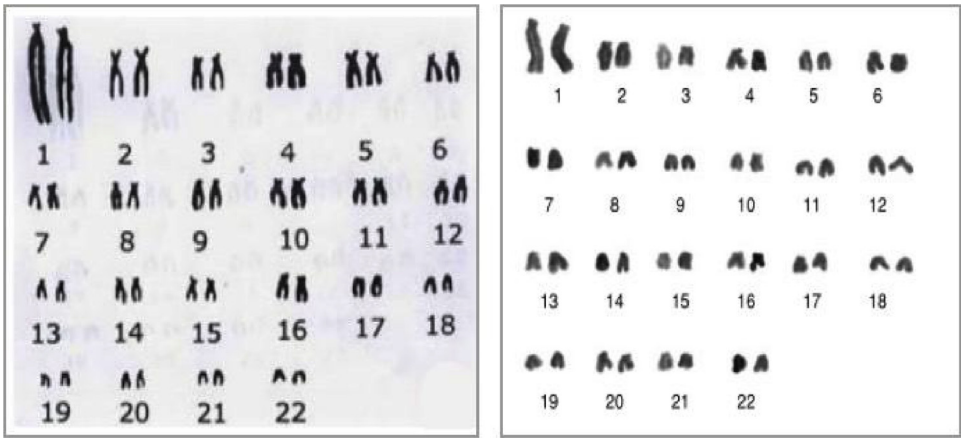


**Fig. 1.** Karyograms of *O. niloticus* (left) and *S. melanotheron* (right) (Harvey et al., 2002b; Manosroi et al., 2003; Sofy et al., 2008).

hybridization between populations of tilapias *Oreochromis aureus* (Israeli strain) and *O. niloticus* (Egyptian strain) did not show significant heterosis when subjected to cold conditions (Behrends et al., 1996). During three generations ($F_1$, $F_2$ and $F_3$), Micha et al. (1996) showed that the heterosis effect on growth is relatively weak for *O. niloticus* and *O. macrochir* hybrids when focusing on their growth. In Côte d'Ivoire, Yapi-Gnaore et al. (1996) recorded negative heterosis for the height and weight (-0.13 cm and -0.22 cm *vs* -0.10 g and -0.31 g) of three *Oreochromis* strains' fry (Bouaké *vs* Egypt and Israel). Also, Attipoe (2006) observed negative heterosis for all diallele crosses of four *O. niloticus*' stocks in Ghana. However, Tayamen et al. (2002) recorded positive percent mean heterosis when crossing *O. mossambicus* x *O. niloticus*, and *O. aureus* x *O. spilurus* (25% *vs* 22%).

### 3.2. Gynogenesis

Gynogenesis consists of producing diploid offspring through a development in which the embryo contains only maternal chromosomes due to activation of an egg by a sperm that does not fuse with the egg nucleus (Castro et al., 2003; Devlin and Nagahama, 2002; Felip et al., 2001). The inactivation of sperm can be carried out by UV irradiation at a dose of 250–265 μW $cm^{-2}$ for 2 min (Sarder et al., 1999). Diploidy is restored by a thermal or pressure shock applied post-fertilization (inhibiting the ejection of the second polar body or suppressing the first mitotic division) (Mélard, 2015). Two types of gynogenesis can occur, involving either meiotic or mitotic chromosomes (Onozato, 1984). To induce meiotic gynogenesis, eggs are heat shocked after fertilization (Sarder et al., 1999). The progeny receive only the maternal chromosomes and if the female is homogametic (XX), the whole gynogenetic offspring will be female (Lee et al., 2003). Gynogenesis can thus, be used to produce completely homozygous individuals in the first generation (Jenneckens et al., 1999; Sarder et al., 1999). On the other hand, if the female is heterogametic (ZW), due to the segregation of different sexual chromosomes, offspring will be WW (females) ZZ (males) and ZW (females) in varying proportions depending on the crossover (second Z or W polar body in a Z or W oocyte). However, gynogenesis is sometimes used to obtain monosex progeny which are then subjected to a hormonal sex-reversal to produce broodstocks having different genotype-phenotype (Ezaz et al., 2004). These gynogenetic stocks are less worthwhile for tilapia production because the technique was too demanding (Jenneckens et al., 1999) and the broods very inbred.

### 3.3. Androgenesis

Relative to gynogenesis, androgenesis is more difficult to implement. The technique has had limited application in aquaculture (Gupta et al., 2004; Shelton, 1997). This method is defined as all-paternal inheritance (Arai, 2001; Kirankumar and Pandian, 2003). Indeed, it consists of the fertilization (by a normal spermatozoid) of an egg whose genetic material has been destroyed by UV irradiation (150 μW $cm^{-2}$ for 4 min) (Sarder et al., 1999) followed by the restoration of the diploidy. The diploidy is restored by the application of a heat shock after fertilization (Myers et al., 1995; Sarder et al., 1999). After application of the heat shock, the resulting diploid androgenetic zygote therefore contains only male derived genetic material (Devlin and Nagahama, 2002).

Androgenesis may be critical to the development of cryopreserved gene banks for fish species (Myers et al., 1995). This technique is used to produce YY 'supermales' very fast in XY systems such as tilapia species (Ezaz et al., 2004). Androgenesis induction is the alternative method of producing genetically induced all-male population in tilapia and other selected fish species to replace hormonal sex-reversal (Hussain, 2004). For ZW species, crosses involving sex-reversed and regular fish can also be used to develop monosex strains in an approach complementary to that described above for XY systems (Devlin and Nagahama, 2002).

## 4. Sex determination systems in tilapia

Two systems of sex-determining chromosomes can be found across tilapia species: the XY system where females are homogametic and the WZ system where they are heterogametic (Harvey et al., 2002a; Mair et al., 1991). In tilapia species, the presence of sexual chromosomes most often is detected through cytogenetics. Much is already known about tilapia genomes. The karyotypes of the various tilapia species are highly similar, consisting in about $1.06 \times 10^9$ base pairs distributed over 22 chromosome pairs ($2n = 44$, Froese and Pauly, 2015; Majumdar and McAndrew, 1986), with no morphologically distinct sex chromosomes (Fig. 1) (Chew et al., 2002; Harvey et al., 2002b; Hussain, 2004; Kocher et al., 1998). Only 10% of teleost fish have differentiated sex chromosomes (Martins et al., 2004; Mélard, 2015). Sex determination is under the influence of environmental factors, genetic factors, behavioural factors and physiological factors (Devlin and Nagahama, 2002). Temperature sex differentiation has been evidenced by Bezault et al. (2011) in natural populations of *O. niloticus* adapted to three extreme thermal regimes.

## 5. Evolutionary and population genetics concepts in tilapias

Understanding the processes that influence the structure of natural populations depends on mastering the basic concepts of population genetics. The loss of genetic variability can have consequences on survival and may drive population to lose its adaptive capacity in case of environmental change due to loss of adaptive alleles or combined

and deleterious allele accumulation (Nikolic et al., 2009a). Changes in abiotic and biotic environmental conditions can alter the direction, strength and form of selection that generates and maintains species differences and species coexistence (Hudson et al., 2013). Several biological and geographical factors can influence tilapia population structure: the sedentary behaviour of the species and mating systems (Amoussou et al., 2018; Bezault et al., 2011; Falk et al., 2003; Laroche et al., 1999; Romana-Eguia et al., 2004; Toguyeni et al., 2007; Yoboue et al., 2014). Because of its substrate affinity during the maternal mouth-brooding and guarding in the reproduction period, *O. niloticus* is considered a sedentary species (Bezault et al., 2011). Moreover, fragmentation of fish habitats can increase the divergence between populations due to gene flow reduction (Laroche and Durand, 2004). As a reminder, several species of tilapia were introduced in many tropical and subtropical countries (Lee et al., 2005). However, these introductions promoted multiple colonization events and hybridization that greatly alters native genetic diversity (Brawand et al., 2014; D'Amato et al., 2007). Due these events, cichlid fishes became enigmatic models for evolutionary and ecological studies.

In population genetics, indices of genetic variability such as allelic richness, genetic differenciation between sub-populations are strongly related to population sizes (De Meeûs, 2012; Griffiths et al., 2013; Hartl and Clark, 2007; Nikolic et al., 2009a; Ollivier et al., 2000). At a local scale, genotypic composition can be compared to the proportion expected under the panmictic model (random union of gametes). In dioecious species like fishes, a small heterozygote excess is expected if adults mate randomly and populations are small (Balloux, 2004). If heterozygote deficits are observed, this may be due to many problems. Some of these are locus specific, like technical problems (null alleles, short-allele dominance, allelic dropout and stuttering), selection (underdominance, assortative mating), but others affect the whole genome equally: inbreeding (sib-mating) or Wahlund effect (admixture in the same sample of genetically heterogeneous individuals) (Baldauf et al., 2013; De Meeûs, 2012; Hartl and Clark, 2007; Pouyaud et al., 1999; Verrier and Rognon, 2000).

The effective population size ($N_e$), a fundamental parameter in population conservation (Nikolic et al., 2009a), affects both the short and long-term evolutionary potential of populations (Amoussou et al., 2018; Bernatchez and Wilson, 1998; Hartl and Clark, 2007). Effective population size determines the rate at which genetic diversity is lost in the population by genetic drift (Hedgecock and Sly, 1990). Everything being equal, subdivision of two populations increases global effective population size (De Meeus et al., 2006; Thomas et al., 2010) because even if local diversity is lost more swiftly, global diversity is maintained much more efficiently (De Meeûs, 2012).

Overall, population genetics principles may be applied to define management and evolutionarily significant units for tilapias. These units can be defined as a population or group of populations that merits priority for conservation and separate management because of high genetic and ecological distinctiveness from other such units. The tilapia units also include the populations that are demographically independent of one another (Hallerman and Hilsdorf, 2014). Population genetics studies were reviewed below.

## 6. Phylogeographic and phylogenetic studies

Phylogeography allows assessing the impact of historical demographic events (such as gene flow, drift, mutation, and evolutionary trajectories) on the genetic composition and structure of modern populations (Avise, 2000; Bernatchez and Wilson, 1998). Phylogenetic establishes the kinship hierarchy among individuals from a group (Gibson and Muse, 2004; Griffiths et al., 2013; Thomas et al., 2010).

Phylogeography and phylogenetic methods are most often used in fish species. Limited genetic information is available on phylogenetic interrelationships or phylogeographic patterns of tilapia species (D'Amato et al., 2007; Falk et al., 2003). For these species, phylogenetic studies are essentially based on allozyme and mtDNA (Abban et al., 2004; D'Amato et al., 2007; Falk et al., 2000; Rognon et al., 1996; Sodsuk and McAndrew, 1991; Sodsuk et al., 1995). RFLP and SSR are rarely used to analyse phylogenetic relationships and phylogeographic patterns of tilapia species (D'Amato et al., 2007; Toniato et al., 2010; Zardoya et al., 1996). One of the few tilapia reports reveals that the Nile Tilapia *O. niloticus* is most likely to have originated in East Africa within the Nile system including Lake Turkana separating early into three groups : the Nile Basin, Lake Tana and Ethiopian Rift Valley (Nyingi and Agnese, 2012). Amoussou et al. (2018) found a significant isolation by distance across *S. melanotheron* subsamples coming from Benin rivers. On the other hand, SSRs were applied to resolve phylogeographic patterns in other fish species (Gum et al., 2005; Koskinen et al., 2002).

## 7. Population or stock management

The decline in fish catches observed in many countries is attributable to many factors such as the increased fishing intensity, pollution, destruction of habitats, introduction of new species and climate change (Amoussou et al., 2017; Dudgeon et al., 2006; Ndiaye et al., 2010). In the past, regulation of the exploitation of the aquatic natural resources has mainly been based on stock abundance evaluations while neglecting the genetic parameters informing about their evolution and viability (Abban et al., 2004; Dudgeon et al., 2012; Nikolic et al., 2009a). Therefore, genetic markers are used nowadays to propose strategies for the management of both wild tilapia populations (Bezault et al., 2011; Hallerman and Hilsdorf, 2014) or cultured tilapia stocks (Ambali and Malekano, 2004; Brinez et al., 2011). *O. niloticus* has been introduced into some African countries such as Benin, Côte d'Ivoire, Niger (Lazard, 1990), Zimbabwe and Zambia (Ambali and Malekano, 2004) because the species grows faster than indigenous species. Owing to poor management, some of these introduced strains have escaped (intentional or not deliberately) into the wild and hybridized with indigenous species (Ambali and Malekano, 2004; Amoussou et al., 2017). In this context, the extent of stock mixing, the relative survival of the different stocks and the extent to which they are disseminated are important issues that need to be addressed for effective management of aquaculture species (Brinez et al., 2011). Bezault et al. (2011) studied the hierarchical patterns of the population genetic structuring of *O. niloticus* in Africa. The dynamic pattern revealed at micro-geographic and temporal scales appears important from a genetic resource management as well as from a biodiversity conservation point of view. Technical guidance has been provided for efficient management *S. melanotheron* species' genetic resources for breeding programs in fresh and brackish waters (Amoussou et al., 2018). Otherwise, two populations units such as evolutionary significant unit (ESU) and Management units (MUs) have been proposed to manage adaptively important genetic variation in wild tilapia populations (Hallerman and Hilsdorf, 2014).

## 8. Genome sequencing and mapping in tilapias

The analysis of genome sequences allows, among other things, determining the functions of genes. Extensive genetic and physical maps, genetic linkage maps, bacterial artificial chromosome (BAC) end sequences, expressed sequence tags (ESTs) are available for tilapias species (Agresti et al., 2000; Cnaani et al., 2002; Guyon et al., 2012; Katagiri et al., 2005; Kocher et al., 1998; Kudo et al., 2015; Lee et al., 2010, 2005). These are developed to support the isolation of genes controlling economically important traits in these species and for annotation of cichlid genome sequences for studies of tilapia physiology, development and evolution (Falk et al., 2003; Katagiri et al., 2005; Kudo et al., 2015; Schliewen et al., 2001). The most complete genetic map for tilapia contains 525 microsatellite and 21 gene-based markers (Fig. 2) spanning a total of 1311 cM (centiMorgans) in 24 linkage groups (Lee et al., 2005).

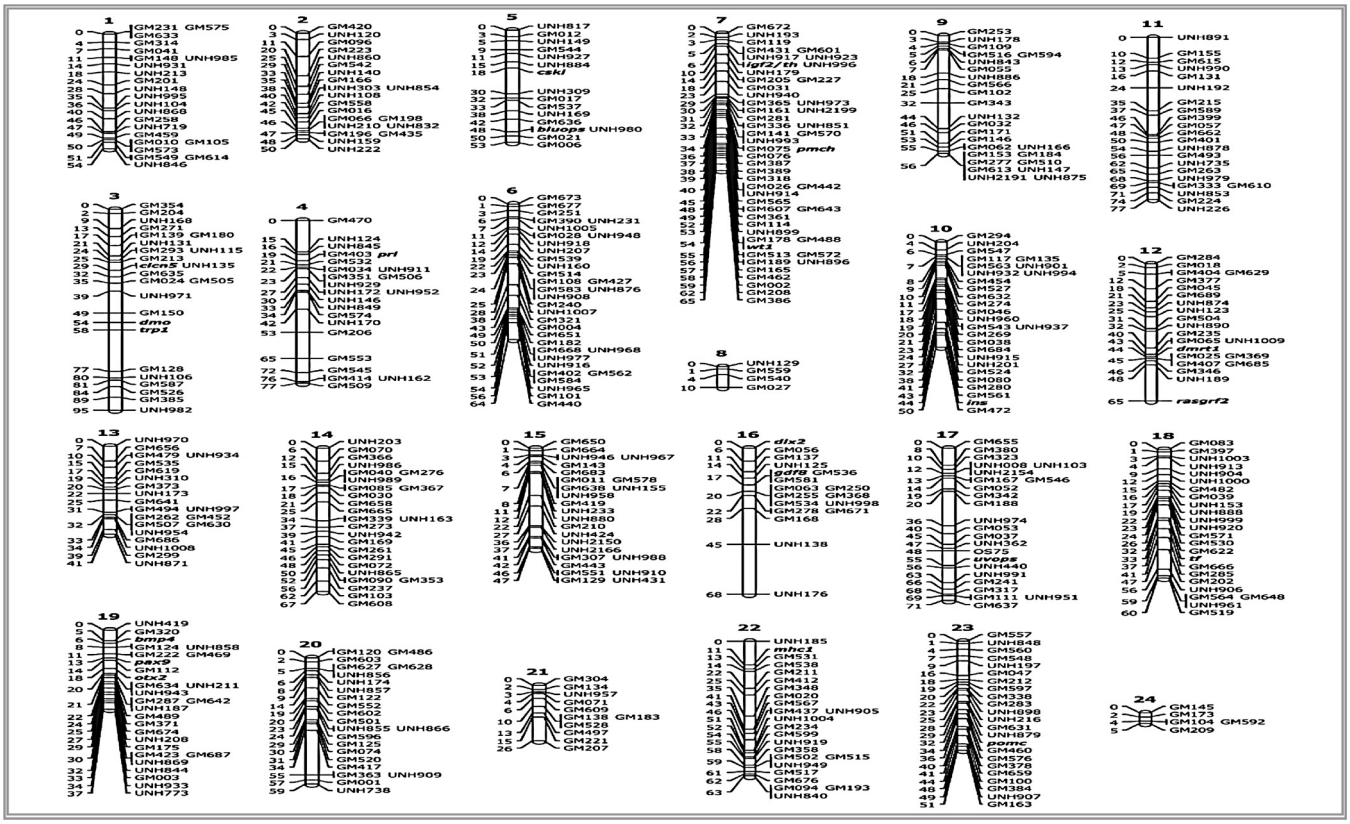

**Fig. 2.** Genetic linkage map for tilapia from the subscript hybrid offspring of a cross between *O. niloticus* and *O. aureus*. Distances in Kosambi centimorgans are given to the left of each ideogram (Lee et al., 2005).

A genome-wide physical map of tilapia, *O. niloticus*, was constructed by restriction fingerprinting of 35,245 BAC clones. It consists of 3621 contigs (partial sequences of DNA derived from the alignment of different fragments of overlapping own sequences, established when sequencing the genome at random) and spans approximately 1.752 Gb in physical length (Katagiri et al., 2005, 2001; Kocher et al., 2005). In addition, a first-generation linkage map of salt tolerant tilapia was constructed using 401 microsatellites. The XY sex-determining loci from Mozambique tilapia and red tilapia were mapped on LG1 and LG22, respectively (Liu et al., 2018). These techniques have been used for mapping and validation of the major sex-determining region in fishes such as Atlantic halibut (*Hippoglossus hippoglossus*) (Palaiokostas et al., 2013), a haplochromine (*Astatotilapia burtoni*) (Böhne et al., 2016). Nowadays, *O. niloticus*'s genome has been sequenced and consist of 2n = 44 chromosomes, 1000 Mb genome size (length), 815 Mb assembled size (length), 2.8 Mb N50 scaffold, and 21,437 number of protein-coding genes (Brawand et al., 2014).

Over the past fifteen years, many genome sequencing consortia have been widely set up, reducing significantly the cost of DNA sequencing and solving the longstanding questions regarding speciation and adaptation in cichlid fishes. During this NGS (next generation-sequencing) era, a process for identifying putative single-copy exons from African cichlid genomes has been described (Ilves and López-Fernández, 2014). It resulted in the sequencing of the targeted exons for a range of divergent (> tens of millions of years) taxa across 10 cichlids including three species from Africa (*O. niloticus*, *Heterochromis multidens*, and *Paratilapia polleni*). Their work evidenced that it is possible to use a relatively divergent reference genome for exon target design and successful capture across a broad phylogenetic range of species. A new method that requires less effort and time has been developed for microsatellite genotyping. The method is called microsatellite genotyping sequencing (SSR-GBS). The approach is based on Illumina and utilizes sequences of amplicons for allele. It has been used to develop 26 microsatellite markers from *O. niloticus* accessions coming from East Africa (Tibihika et al., 2018). Next-generation sequencing technologies also include *De novo* assembly of transcript sequences that offers a rapid approach to obtain expressed gene sequences for non-model organisms. The approach facilitates the development of quantitative real-time PCR (qPCR) assays for analysing gene expression under different environmental conditions. Through this technique, a transcriptomic web resource has been created for *S. melanotheron* to provide a useful tool for functional genomics and genetics studies (Avarre et al., 2014). Another study evidenced that intestinal transcriptome analysis revealed differential salinity adaptation between two *O. mossambicus* (high salinity-tolerant) and *O. niloticus* (less salinity-tolerant). There is high similarity in gene expression response to salinity change between *O. mossambicus* and *O. niloticus* in the posterior intestine and large differences in the anterior intestine. In the anterior intestine, 68 genes were saltwater up-regulated in one species and down-regulated in the other species (47 genes up-regulated in *O. niloticus* and down-regulated in *O. mossambicus*, with 21 genes showing the reverse pattern) (Ronkin et al., 2015).

## 9. Genetic markers

The different genetic markers reviewed in this paper are presented in Table 2. There are two types of genetic markers, phenotypic markers and genomic markers. Proteins are phenotypic markers, while DNA sequences are regrouped as genomic markers (Griffiths et al., 2013; Watson et al., 2012). In population genetics, to be useful, a genetic marker must be transmitted in a Mendelian way, polymorphic (variable between individuals), discriminating (differentiates related individuals), neutral (i.e. strictly reflecting demographic parameters such as reproductive system, dispersal, sub-population size, etc.), reproducible from one experiment to another, usable on large-scales (spatial or temporal) and economic (De Meeûs, 2012; Nikolic et al., 2009a, 2009b). However, for studies on phenotypic traits to select (for

**Table 2**
Characteristics and applications of different DNA markers in tilapias.

| Marker type and it acronym | Mode of inheritance | Phenotypic or genomic markers | Locus under investigation | Likely allele numbers | Polymorphism or power | Major applications | Source |
|---|---|---|---|---|---|---|---|
| Allozyme | Mendelian, codominant | Phenotypic marker | Multiple | 1–6 | Low | Population studies, Phylogenetics | Adépo-Gourène et al. (1998); Agnèse et al. (1997); Appleyard et al. (2001); De Silva (1997); Gourène and Agnese (1994); Liu and Cordes (2004); Pouyaud and Agnèse (1994); Rognon et al. (1996); Rognon and Guyomard (2003); Yoboué et al. (2012) |
| Amplified fragment length polymorphism (AFLP) | Mendelian, Dominant | Genomic marker | Multiple | Multiple | High | Fingerprinting, Linkage mapping, Population studies | Agresti et al. (2000); Kocher et al. (1998); Liu and Cordes (2004); Nyingi et al. (2009) |
| Expressed sequence tags (EST) | Mendelian, Codominant | Phenotypic marker | Multiple | 2 | Low | Linkage mapping, Physical mapping, Comparative mapping | Lee et al. (2010); Liu and Cordes (2004); Watanabe et al. (2004) |
| Insertions/deletions (Indels) | Mendelian, Codominant | Phenotypic or Genomic marker | Multiple | 2 | Low | Linkage mapping, Population studies | Falk et al. (2003); Liu and Cordes (2004); Rengmark and Lingaas (2007); Schliewen and Klee (2004); Szitenberg et al. (2012) |
| Microsatellites (SSR) | Mendelian, Codominant | Genomic marker | Multiple | Multiple | High | Fingerprinting, Linkage mapping, Population studies, Paternity analysis, Phylogeography | Adépo-Gourène et al. (1998); Agresti et al. (2000); Amoussou et al. (2018); Appleyard et al. (2001); Bezault et al. (2011); Brinez et al. (2011); Kocher et al. (1998); Liu and Cordes (2004); Yoboue et al. (2014) |
| Minisatellite (VNTR) | Mendelian, Codominant | Genomic marker | Multiple | Multiple | High | Fingerprinting, Genome mapping, Population studies, Evolutionary conservation, Breeding and selection programs, Ecological and conservation biology, Phylogenetics | Bentzen et al. (1991); Bentzen and Wright (1993); Harris and Wright (1995); Richard et al. (2008) |
| Mitochondrial DNA (mtDNA) | Maternal Inheritance | Genomic marker | Multiple | Multiple Haplotypes | Low | Maternal lineage, Phylogeography, Phylogeny, Population studies | Agnèse et al. (1997); Avise (2000); Dunz and Schliewen (2013); Falk et al. (2003); Falk and Abban (2004); Liu and Cordes (2004); Nyingi and Agnese (2012); Rognon and Guyomard (2003) |
| Random amplified polymorphic DNA (RAPD) | Mendelian, Dominant | Genomic marker | Multiple | 2 | Intermediate | Parentage assessment, Population studies, Hybrid identification | Bardakci and Skibinski (1994); Liu and Cordes (2004); Usman et al. (2013) |
| Restriction fragment length polymorphism (RFLP) | Mendelian, Codominant | Phenotypic or Genomic marker | Multiple | Mostly bi-allelic | Low | Linkage mapping, Population studies, Phylogeny | Askari et al. (2013); Bernatchez and Wilson (1998); Liu and Cordes (2004); Meyer (1993) |
| Single nucleotide Polymorphism (SNP) | Mendelian, Codominant | Phenotypic or Genomic marker | Multiple | 2, but up to 4 | High only if numerous loci are used | Linkage mapping, Population studies | Brawand et al. (2014); Guyon et al. (2012); Liu and Cordes (2004) |
| Single Strand Conformation Polymorphism (SSCP) | Mendelian, Codominant | Genomic marker | Multiple | 2 | Low | Linkage mapping, Population studies | Gibson and Muse (2004); Liu and Cordes (2004); Rodrigues et al. (2014) |

example, selective breeding), a genetic marker must be epistasis free (independent of the expression of other markers). The assessment of the within and among-species genetic variability requires other properties for the genetic markers used: their ubiquity throughout the genome and the possibility of automating their identification (Ollivier et al., 2000). For population genetics studies, it is recommended to use a large number of loci (7–20 for microsatellites, 10–20 for allozymes or much more for SNPs) because data based on a relatively small number of loci may not provide an accurate indication of the genetic variation level within individuals, populations and species (Lee and Kocher, 2007).

Genetic markers are powerful tools that have received various applications: to map the genome, to study population genetics, to detect loci coding for quantitative or qualitative characters, to specify the location of genes responsible for hereditary diseases, to realize pre-natal diagnostics of hereditary diseases (Chistiakov et al., 2006; Ferguson et al., 1995; Hossain et al., 2012; Liu and Cordes, 2004; Schmouth et al., 2015).

Allozymes, AFLPs, indels, SSRs, Minisatellites, mtDNA, RAPDs, RFLPs, SNPs and SSCPs have been used for tilapia population management and conservation (Adöpo-Gourène et al., 1998; Agresti et al., 2000; Amoussou et al., 2018; Appleyard et al., 2001; Bezault et al., 2011; Brinez et al., 2011; Ferguson et al., 1995; Lazard, 2013; Liu and Cordes, 2004; Rognon et al., 1996; Yoboue et al., 2014).

### 9.1. Allozyme markers

These are enzymes that differ in electrophoretic mobility as a result of allelic differences in a the corresponding gene (Hartl and Clark, 2007) and characterized histologically after electrophoresis of proteins on a gel (De Meeûs, 2012). These markers are very cheap and easy to handle (De Meeûs et al., 2007). Nevertheless, allozymic loci are generally weakly polymorphic (Appleyard et al., 2001; Romana-Eguia et al., 2004). Other disadvantages are associated with allozymes. Occasional heterozygote deficiencies are due to null (enzymatically inactive) alleles (Gaffney, 1994; Skalamera et al., 1999). They are sensitive to the quantity as well as quality of tissue samples (Askari et al., 2013; Brown and Epifanio, 2003; Larsson et al., 2007; Liu and Cordes, 2004). Allozymes correspond to coding sequence and as such were frequently suspected to reflect more selective than demographic events (Karl and Avise, 1992; Lemaire et al., 2000; Skalamera et al., 1999). Additionally, these markers present considerable disadvantages for sample collection and storage (fish need to be killed in most cases; tissues need to be kept frozen until analysed) in comparison with DNA markers amplified by PCR (small biopsies are generally sufficient; these can be stored in ethanol without freezing) (Romana-Eguia et al., 2004; Toniato et al., 2010). Nevertheless, allozyme markers and performance traits sometimes are correlated (McGoldrick and Hedgecock, 1997).

Allozymes can be used as tilapia population management and conservation tools (Adépo-Gourène et al., 1998; Agnèse et al., 1997; Appleyard et al., 2001; De Silva, 1997; Gourène and Agnese, 1994; Pouyaud and Agnèse, 1994; Rognon et al., 1996; Rognon and Guyomard, 2003; Yoboué et al., 2012). A survey in western and eastern Africa enabled visualize of polymorphism of allozymes in *Coptodon zillii*, in wild Nile tilapia (*O. niloticus*) and in cultured Nile tilapia stocks (Rognon et al., 1996). Authors have observed the same pattern of geographical differentiation between the west and east African populations in both species. A study was carried out on genetic diversity and adaptatibility of *S. melanotheron melanotheron* and *S. melanotheron heudelotii* in the coastal ecosystem of Senegal, Gambia and Ivoiry Coast with seven enzymatic markers (Yoboué et al., 2012). The genetic variability of *S. melanotheron melanotheron* in the Ivorian ecosystem was lower than that of *S. melanotheron heudelotii* of Gambia (Gambia) and Saloum (Senegal) estuaries. In another study (Appleyard et al., 2001), no relationship was found between allozyme multilocus heterozygosity (MLH) and individual growth performance across three generations and selecting *O. niloticus* broodstocks based solely on the level of individual MLH is thus unlikely to improve relative growth performance.

### 9.2. Restriction fragment length polymorphism (RFLP) markers

The principle of RFLP is based on the polymorphism of DNA fragments size due to the mutations (nucleotidic substitutions, insertions, deletions) occurring at restriction enzyme sites between individuals of a species (Liu and Cordes, 2004). Restriction enzymes cut the DNA at specific sequences, and migration of the resulting fragments depends on their size (Gibson and Muse, 2004; Hartl and Clark, 2007). When genomic DNA of different strains is digested with the same restriction enzyme, each gives rise to a slightly different assortment of restriction fragment sizes; Each variation is called a RFLP. Southern blot hybridization with a 32P-labelled probe, is used to selectively visualize restriction fragments that often vary in size. Because RFLPs are abundant in the genome of most organisms, they have received numerous applications in analyses of fish population genetics. There are, however, several limitations for RFLP analysis (Semagn et al., 2006): It requires the presence of high quantity and quality of DNA; It depends on the development of specific probe libraries for the species; The technique is not amenable for automation; The level of polymorphism is low, and few loci are detected per assay; It is time-consuming, laborious, and expensive; It usually requires radioactively labelled probes.

RFLP analysis has proven useful in clarifying relationships among closely related fish species (Askari et al., 2013; Bernatchez and Wilson, 1998; Liu and Cordes, 2004; Meyer, 1993). The spatial distribution of populations of *O. niloticus* and *O. aureus* from Western, Central, Northern and Eastern Africa were analysed through RFLPs (Agnèse et al., 1997). The network obtained showed that there are three geographically distinct groups; all West African populations are clustered; the two Ethiopian Rift Valley populations are distinct, and between these two groups are the Kenyan and Ugandan Rift Valley populations. Nile populations show affinities with both West African populations and specimens from Lakes Tana and Turkana (Agnèse et al., 1997). In Burkina Faso, these markers permitted investigation of the genetic structure of the domestic and wild populations of the Nile tilapia, *O. niloticus* (Toguyeni et al., 2007). It appears that the populations of Bazèga could have been introgressed by those coming from Kompienga. Some individuals of Kompienga population are to be maintained in the same rearing station of Bazèga. Bazega and Kompienga are located in Burkina Faso.

### 9.3. Mitochondrial DNA (mtDNA) markers

The mtDNA is a small circular DNA ranging in length from 15 to 20 kb. Having a mutation rate 5 to 10 times greater than nuclear DNA, mtDNA has often been used to make inferences about population structure and recent population history (Hartl and Clark, 2007). mtDNA is analyzed at the sequence level for genes like cytochrome oxidase I (cox1) and cytochrome *b* (CytB) (Dudgeon et al., 2012; Liu and Cordes, 2004; Papadopoulou et al., 2010). For Cytb, this gene has some limitations as a phylogenetic marker, and it fails to resolve the lower genetic relationships in cichlid fishes because of its slow mutation rate (Soliman et al., 2017). These markers are haploid; hence do not give access to local heterozygosity.

mtDNA never or rarely recombines (Birky, 2001), and hence all mtDNA markers are linked to the same fate. Similarly, the application of mtDNA studying hybridization and introgression is limited due to its maternal inheritance (Toniato et al., 2010). For this reason, mtDNAs are more useful for phylogeographic studies than for populations genetics studies (De Meeûs, 2012; Falk et al., 2003).

Several studies based on mtDNA markers have been used to assess genetic structure, phylogeny, demographic and phylogeographic patterns at intraspecific scales (Agnèse et al., 1997; Avise, 2000; Dunz and Schliewen, 2013; Falk et al., 2003; Falk and Abban, 2004; Nyingi and Agnese, 2012; Rognon and Guyomard, 2003; Toguyeni et al., 2007).

These investigations have unveiled three geographically distinct groups of *O. niloticus* in Africa: West African populations, Kenyan, and Ugandan Rift Valley populations (Agnèse et al., 1997; Nyingi and Agnese, 2012). Rognon and Guyomard (2003) pointed out a differential introgression of mtDNA from *Oreochromis aureus* to *O. niloticus* involving all the West African area. In the Volta system of Ghana, genetic divergences were found for *O. niloticus* individuals from the southern areas (Kpandu/Kope and Yeji/Pru) (Falk and Abban, 2004). *O. niloticus* populations are genetically heterogeneous in Burkina Faso (Toguyeni et al., 2007).

*S. melanotheron* includes three subspecies: *S. melanotheron heudelotii* (Dumeril, 1859) known from Senegal to Guinea, *S. melanotheron leonensis* (Thys van den Audenaerde, 1971) known from Sierra Leone to western Liberia and *S. melanotheron melanotheron* Rüppell, 1852 found from Ivory Coast to Benin (Falk et al., 2003). This brought genetically support for the existence of *S. melanotheron leonensis* for the first time.

Dunz and Schliewen (2013) provided a revised classification of the paraphyletic tilapiine assemblage. New tribes were proposed for the former subgenera *Coptodon* Gervais, 1853, *Heterotilapia* Regan, 1920 and *Pelmatolapia* Thys van den Audenaerde, 1969, in addition to "*Tilapia*" *joka*, *Tilapia* sensu stricto and *Chilochromis*, *Etia*, *Steatocranus* sensu stricto, the mouth-brooding tilapiines, and for a clade of West African tilapiines.

### 9.4. Random amplified polymorphic DNA (RAPD) markers

Developed in 1990 (Welsh and McClelland, 1990; Williams et al., 1990), randomly amplified polymorphic DNA (RAPD) is revealed after the amplification of the total genome by a battery of small primers that anneal anywhere there are two complementary sequences. If two of these primers are close enough together, the fragment between them will be amplified. RAPDs are thus dominant markers assumed to be selectively neutral (Dudgeon et al., 2012). The major asset of RAPD markers is the speed with which it is possible to reveal a large number of loci and for large numbers of individuals (Lynch and Milligan, 1994), with the added benefit that primers are commercially available and do not require prior knowledge of the target DNA sequence or gene organization (Dudgeon et al., 2012; Liu and Cordes, 2004). They are also cheap. By their random nature, it is impossible to know what the different DNA portions amplified by RAPD correspond to. It is therefore impossible to know whether these loci are in genes or not, what are their mutation rates, etc. (De Meeûs, 2012). RAPDs also have the disadvantage of being poorly reproducible because of stochastic variations of amplification cycles' efficiency (the low annealing temperature used in PCR amplification) and differences in protocols among laboratories (Dudgeon et al., 2012). These difficulties have braked the application of these markers in fisheries science (Askari et al., 2013). Despite this, they have been used for tilapia population studies (*O. niloticus*, *S. melanotheron*, and *T. guineensis*) and species identification (Bardakci and Skibinski, 1994; Usman et al., 2013). Bardakci and Skibinski (1994) showed that RAPD markers might be useful for tilapia identifications at the species and subspecies levels. RAPDs were also used to compare genetic variability among tilapia species in Nigeria (Usman et al., 2013).

### 9.5. Amplified fragment length polymorphism (AFLP) markers

Developed in 1995, the AFLP technique constitutes a variant of RFLP (Vos et al., 1995). In the last decade, AFLPs most often were used to study the genetic structure of natural populations (Foll et al., 2010). The principle is based on the selective amplification of DNA fragments generated by digestion by a combination of two restriction enzymes, e.g. *MseI* and *EcoRI* (Liu and Cordes, 2004). Adapters then are added to the extremities of cleavage sites so that PCR primers can bind to the digested fragments. AFLPs are applicable to any species, including less well-studied fish species (Liu and Cordes, 2004). They are dominant markers.

AFLPs have proven useful to genetically characterise populations of *O. niloticus* (Nyingi et al., 2009). In the aim to detect quantitative trait loci (QTL) in tilapias for aquaculture, linkage genetic maps (schematic diagrams showing the location of genes on chromosomes) were developed with AFLP and microsatellite loci for cold and salinity tolerance and carcass quality (Agresti et al., 2000; Kocher et al., 1998). Kocher et al. (1998) identified linkages among 93.1% of the tested markers. In addition, 95% of the microsatellites and 92% of the AFLPs were linked in the final linkage map constructed. The map spans 704 Kosambi centimorgans in 30 linkage groups covering the 22 chromosomes of *O. niloticus*. Agresti et al. (2000) noted that when scoring AFLP markers, we are scoring alleles and not necessarily loci. Indeed, there are many cases where two adjacent polymorphisms from the same primer combination show absolute linkage on the map. It is likely that these are actually alleles at the same locus.

### 9.6. Minisatellite markers (VNTRs)

Minisatellites or Variable Number Tandem Repeats (VNTR) are sequences of tandem repeats whose repetitions are long of about 9 to 65 base pairs in eukaryotic genomes (Harris and Wright, 1995; Richard et al., 2008). The number of these repetitions varies from an individual to another and constitutes a set of alleles. Like microsatellite markers, minisatellite alleles are Mendelian (Harris and Wright, 1995; O'reilly and Wright, 1995). VNTRs exhibit extremely high rates of mutation (Wright, 1994), leading to large polymorphism rates in natural populations.

Minisatellites received various applications in fish studies, mostly for salmonids and tilapias, DNA fingerprinting and evolutionary conservation (Bentzen et al., 1991; Bentzen and Wright, 1993; Harris and Wright, 1995). They were also used for *O. niloticus* population studies (Harris et al., 1991; Harris and Wright, 1995). The results of Harris et al. (1991) in aquaculture genetics included assessment of inbreeding rates, individual and family group identifications and the labelling of broodstocks to secure ownership.

### 9.7. Microsatellite markers (SSRs or VNTRs)

Also called Simple Sequence Repeats (SSR) or Variable Number Tandem Repeats (VNTR) (which also applies to minisatellite markers), microsatellite markers are short tandemly repeated DNA sequences distributed throughout the genome and, most of the time, without known function (De Meeûs, 2012). The DNA sequence is composed by the repetition of some (1–9) nucleotides (Richard et al., 2008), as the dinucleotide –CA- or the trinucleotide –CGG- (Carleton et al., 2002; Watson et al., 2012). The technique requires relatively small quantities of biological material for screening an individual, and often show higher variability than other markers (Estoup et al., 1998; Romana-Eguia et al., 2004). Their great variability is due to high mutation rates, ranging from 0.01 to 0.0001 (Balloux and Lugon-Moulin, 2002; Ellegren, 2004). They are mostly used at the intraspecific level for population genetic structure studies and the inference of the historic events that occurred within populations of living organisms (Lee and Kocher, 1996; Liu and Cordes, 2004). These markers also provide valuable tools for a wide range of genetic investigations. They allow species comparison using PCR primers developed in one species and cross-amplified in closely related taxa (Amoussou et al., 2018; Bezault et al., 2012, 2011). They are also useful for linkage mapping, parentage or forensic analyses (Ellegren, 2004). High levels of polymorphism give microsatellite markers high discriminating power (Toniato et al., 2010; Wright and Bentzen, 1994). In fisheries and aquaculture, microsatellite markers are useful for the characterization of genetic stocks, broodstock selection, constructing dense linkage maps, mapping economically important quantitative traits, identifying genes responsible for these traits, for marker assisted-breeding programmes (Bentzen et al., 1991;

Chistiakov et al., 2006) and searching for sex determination controlling genes (Lee et al., 2003).

Microsatellites received numerous applications in the characterization and genome mapping of tilapia species like *O. niloticus*, *S. melanotheron*, *O. aureus*, *O. mossambicus*, and *S. galilaeus* (Adépo-Gourène et al., 1998; Agresti et al., 2000; Amoussou et al., 2018; Appleyard et al., 2001; Bezault et al., 2011; Brinez et al., 2011; Kocher et al., 1998; Yoboue et al., 2014). To support the management of stocks, Kocher et al. (1998) constructed a genetic map for *O. niloticus*, using SSRs. 95% of the microsatellites were linked in the map, and 24 of the linkage groups contain at least one microsatellite polymorphism. Adépo-Gourène et al. (1998) showed that the West African populations of *S. melanotheron* are genetically different. Appleyard et al. (2001) observed that no significant correlations with either length or weight were observed at several microsatellite loci tested. The authors therefore suggest that selecting brood-stocks based solely on individual's microsatellite heterozygosity levels is unlikely to increase relative growth performance in the Fijian cultured *O. niloticus*. Using SSRs, Brinez et al. (2011) evaluated the genetic diversity of six populations of red hybrid tilapia from Colombia. The results showed that the samples are differentiated genetically, and it is possible to use them purposely at the beginning of a genetic program. On the other hand, the genetic diversity and structure of *S. melanotheron* samples representing endemic subspecies of West Africa, *S. melanotheron melanotheron* (Amoussou et al., 2018; Yoboue et al., 2014) and *S. melanotheron heudelotii* (Yoboue et al., 2014), were studied using microsatellite markers. Significant genetic differentiation was observed between the studied populations.

### 9.8. Expressed sequence tags (ESTs)

ESTs are short DNA of sequences (often 200–800 nucleotide bases in length) derived from a random group of reverse transcription of mRNA molecules: they are therefore complementary DNA (Gibson and Muse, 2004; Hartl and Clark, 2007; Nagaraj et al., 2007; Tagu and Risler, 2010). Sequencing of both 5′- and 3′-ends of cDNA clones to generate ESTs is the most efficient method for gene discovery (Askari et al., 2013; Chistiakov et al., 2006; Lee and Kocher, 2007). Generally, ESTs enable gene discovery, complement genome annotation, gene structure identification, establishing the viability of alternative transcripts, guide RFLP, SSR and SNP characterization and facilitate proteome analysis (Liu, 2007; Nagaraj et al., 2007; Semagn et al., 2006). ESTs are useful for mapping fish species' genome in aquaculture (Liu and Cordes, 2004). Large numbers of ESTs have been developed for closely related species of haplochromine cichlids from East Africa (Watanabe et al., 2004). Similarly, an extensive collection of ESTs (116,899) from 19 cDNA libraries representing 16 tissues from tilapia was constructed for *O. niloticus* (Lee et al., 2010) in order to support the studies of gene expression, comparative mapping and annotation of the tilapia genome sequence.

### 9.9. Single-Strand Conformation Polymorphism (SSCPs)

SSCPs use the capacity of any single-stranded nucleic acid to constitute intra-molecular base pairs, for SNP discovery (Gibson and Muse, 2004; Liu and Cordes, 2004). Indeed, SSCP relies on the fact that within a short DNA segment (usually no more than 300 base pairs), a single base-change in the sequence can cause major changes in single-stranded conformation that is a reflection of the secondary structure of single-stranded DNA upon hairpin formation and minor base pairings (Liu, 2007; Vignal et al., 2002). Technically, the amplified PCR product is denatured in a weakly alkaline solution and then deposited on an acrylamide gel (8%). Then, electrophoresis is performed (Chenuil, 2006; Gibson and Muse, 2004; Nguyen et al., 2006a; Semagn et al., 2006).

SSCPs have been used for genotyping three strains (GIFT, Chitralada and Supreme) of *O. niloticus* (Rodrigues et al., 2014). Three polymorphisms were identified in a portion of the regulatory region for the ovarian aromatase gene (CYP19a), resulting in two different sequences, in the GIFT strain, while no polymorphism was found in both Supreme and Chitralada strains.

### 9.10. Single nucleotide polymorphism (SNP)

SNP is a site in the genome at which there is a single nucleotide having two, and less frequently 3 or 4, different states within a collection of individuals of the same species (Gibson and Muse, 2004). For example, some DNA molecules in a population may have a T (thymidine) nucleotide at this site, whereas other DNA molecules in the same population may have a C (cytosine) nucleotide at the same site (Hartl and Clark, 2007). SNPs are useful in population genetics (Griffiths et al., 2013; Hartl and Clark, 2007). The fact that mutation rates are very low and that transversions are half likely than transitions makes SNPs functionally bi-allelic (Askari et al., 2013; De Meeûs, 2012; Liu and Cordes, 2004; Vignal et al., 2002). SNPs are informative but their analysis is still expensive and requires the study of many loci for achieving considerable experimental power, depending on sample sizes: up to 500 may be needed, though inbreeding and relatedness will still remain difficult to estimate accurately (Morin et al., 2009; Smouse, 2010).

The use of SNPs to study tilapias' genetics is still rare. However, a set of genome wide SNPs available for Nile tilapia has been developed by Guyon et al. (2012) and Brawand et al. (2014). Guyon et al. (2012) have genotyped 1358 markers consisting of 850 genes, 82 markers corresponding to BAC end sequences, 154 microsatellites and 272 single nucleotide polymorphisms (SNPs). Brawand et al. (2014) have sequenced the genomes and transcriptomes of five lineages of African cichlids: the Nile tilapia (*O. niloticus*), *Neolamprologus brichardi/pulcher*, *Metriaclima zebra*, *Pundamilia nyererei* (very recent radiation, Lake Victoria), and *Astatotilapia burtoni* (riverine species around Lake Tanganyika). They found an excess of gene duplications in the East African lineage compared to tilapia and other teleosts, accelerated coding sequence evolution, expression divergence associated with transposable element insertions, and regulation by novel microRNAs. The authors concluded that a number of molecular mechanisms have shaped East African cichlid genomes, and that amassing of standing variation during periods of relaxed purifying selection may have been important in facilitating subsequent evolutionary diversification. Xia et al. (2014) have identified 23,535 high quality SNPs located in 7146 genes *O. niloticus*. They also evidenced that red tilapia is a hybrid admixture of different resources of tilapias. Nowadays, the total available high-quality SNPs identified in *O. niloticus* is 1.43 million (Xia et al., 2015).

### 9.11. Insertions/deletions (Indels)

An Indel is a mutation that consists of the insertion or deletion of one or more nucleotides in DNA, RNA, or amino acids in proteins, which are frequently observed in sequence alignments (Griffiths et al., 2013; Thomas et al., 2010). Indels of one base are considered SNPs (Gibson and Muse, 2004; Griffiths et al., 2013). Thus, many SNP detection techniques also can be used for scoring small indels (Vignal et al., 2002). Smaller indels require DNA sequencing or more elaborate electrophoretic techniques to determine smaller changes in size (Liu and Cordes, 2004). The variation often detected in allozymes, mtDNAs, RAPDs, AFLPs and RFLPs may be the result of indels (Liu, 2007; Liu and Cordes, 2004; Schliewen and Klee, 2004).

The possibility of detecting indels in the genomes of many tilapia species have been investigated: *T. zillii* (Szitenberg et al., 2012), *S. melanotheron*, *S. nigripinnis*, *O. niloticus*, *S. galilaeus* (Falk et al., 2003; Schliewen and Klee, 2004) and *O. niloticus* (Rengmark and Lingaas, 2007). Szitenberg et al. (2012) explored the genetic and morphological variation of *T. zillii*, using mitochondrial control region sequences and meristic characters. The DNA fragments were sequenced on both strands. The indels were detected manually by looking at the

corresponding region on the chromatogram. The final alignment included two indels. When focusing on the 58 different mtDNA haplotypes identified within the sequenced part of the mitochondrial control region (372–377 bp), Falk et al. (2003) built a neighbour-joining tree for *S. melanotheron* and *S. nigripinnis* populations of West and Central Africa. Several indels were detected. Several indels also were observed in the sequence alignments of the transferrin gene of *O. niloticus* (Rengmark and Lingaas, 2007). However, no indels larger than 1 basepair (bp) were detected in the genome of *S. galilaeus* populations from the crater lakes of Cameroon (Schliewen and Klee, 2004).

## 10. Conclusion

Using a genetic marker is conditioned by the facilities available, the research objectives, and the quality-price ratio. The most-used molecular markers for *O. niloticus* and *S. melanotheron* studies are currently mtDNA and SSR. Allozymic and RFLP are in little if any current use. Mitochondrial, SSRs, ISSRs and SNPs are promising tools for tilapia genetic characterization notably in their fingerprinting, linkage mapping, population genetic studies, and paternity analyses. AFLPs are just too tedious, and results are hard to pool across runs and laboratories. It also appears essential to compare the genomes of these two tilapia species to identify the genes underlying their remarkable diversity of morphology and behaviour. The DNA barcoding in tilapia characterization is proving to be a useful tool in the identification of cryptic tilapia species.

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